

Permeability of habitat edges for Ringlet butterflies (Lepidoptera, Nymphalidae, *Erebia* Dalman 1816) in an alpine landscape

ANDREA GRILL¹, DANIELA POLIC², ELIA GUARIENTO³, KONRAD FIEDLER⁴

¹ Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

² Department of Biology and Environmental Science, Linnaeus University, Hus Vita, SWE-44050, Kalmar, Sweden

³ Institute for Alpine Environment, Eurac Research, Viale Druso 1, IT-39100 Bolzano / Bozen, Italy

⁴ Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, A-1030 Wien, Austria

<http://zoobank.org/FEB59D1E-DC09-4A9F-9117-B3BE8EC405C1>

Received 28 June 2019; accepted 27 November 2019; published: 14 February 2020

Subject Editor: Martin Wiemers.

Abstract. We tracked the movements of adult Ringlet butterflies (Lepidoptera, Nymphalidae, *Erebia* Dalman, 1816) in high-elevation (> 1800 meters a.s.l.) grasslands in the Austrian Alps in order to test if an anthropogenic boundary (= an asphalt road) had a stronger effect on butterfly movement than natural habitat boundaries (trees, scree, or dwarf shrubs surrounding grassland sites). 373 individuals (136 females, 237 males) belonging to 11 *Erebia* species were observed in one flight season (July–August 2013) while approaching or crossing habitat edges. *Erebia pandrose* (Borkhausen, 1788) was the most abundant species with 239 observations. All species studied were reluctant to cross habitat boundaries, but permeability was further strongly affected by the border type. Additional variables influencing movement probability were species identity and the time of the day. In *E. pandrose*, for which we had sufficient observations to analyse this, individuals were more likely to cross a boundary in the morning and in the late afternoon than at midday. *Erebia euryale* (Esper, 1805) and *E. nivalis* Lorković & de Lesse, 1954 were more likely to leave a habitat patch than their studied congeners. The key result of our study is that the paved road had the lowest permeability among all edge types (0.1 likelihood of crossing when approaching the edge). A road cutting across a conservation area (viz. a national park) thus hinders inter-patch exchange among Ringlet butterflies in the alpine zone, even though theoretically they ought to be able to fly across.

Introduction

An “edge” can be defined as any boundary between two ecosystems inhabited by different biological communities or as “transitional zones between adjoining ecosystems or habitats” (e.g., Magura et al. 2017 and references therein). In alpine landscapes, which are the focus of this study, natural edges exist, for instance, where grasslands border scree, shrubs, or woodland. Alternatively, there are anthropogenic edges, like roads crossing a habitat or the borders to areas under different modes of land-use. Most anthropogenic edges are characterized by sharper environmental contrasts and have been described to be less permeable than natural ones in a number of studies (e.g., Ascensão et al. 2017 for mammals; Magura et al. 2017 for beetles; Baguette and Van Dyck 2007 for insects; Ries and Debinski 2001 and Polic et al. 2014 for butterflies). Permeability is a term coined by movement ecologists and usually defined as “the degree to which a barrier inhibits movement” (Beyer et al. 2016); where a barrier is a feature in the landscape that can be “crossed but not circumnavigated”. Various animal groups living in vegetated habitats, such as small mammals (Ascensão et al. 2017), amphibians (Matos et al. 2017) and elephants (Wadey et al. 2018) have

been reported to avoid areas lacking vegetation cover. It has been suggested that this avoidance behaviour is innate to terrestrial organisms living in vegetated habitats. Consequently, depending on species-specific responses vegetation-free elements may even act as complete barriers for animals when moving through the landscape (Beyer *et al.* 2016). Among the most impermeable edges are asphalted linear infrastructures ubiquitous worldwide: roads (Forman *et al.* 2003; van der Ree *et al.* 2015). In winged animals, data on how movement behaviour is affected by roads have so far been collected mainly for birds (Lima *et al.* 2015; Rytwinski and Fahrig 2015) which clearly react to roads and were even found to adjust their flight behaviour to speed limits of traffic on roads (Legagneux and Ducatez 2013), and to reduce the amount of parental care given to fledgelings (e.g., Ng *et al.* 2019) when living next to a road. In insects, such data are even more limited, especially for habitats outside the usual European lowlands under more or less intense agricultural use (Muñoz *et al.* 2015; Jacobson *et al.* 2016; Andersson *et al.* 2017). Together with a previous study in 2012 (Polic *et al.* 2014) we were the first to attempt to obtain data on the effect of a road on the movement of *Erebia* Dalman, 1816 butterflies in high elevation grasslands.

Whereas our first study was a mark-release-recapture experiment, we now focused on tracking the movement of individual un-manipulated adult butterflies at four edge types bordering their natural grassland habitats: (a) trees, (b) scree, (c) dwarf shrubs, (d) roads. Eleven *Erebia* species that we knew to be present in the area were chosen as target species for observation (see Table 1 for list of species).

We hypothesized that the anthropogenic boundary (i.e., the asphalt road) would have a lower permeability than the natural boundaries and that this effect would be similar for all studied species in this butterfly genus. We also tested if the time of the day affected the likelihood of crossing a border as it has been suggested that temporal changes in activity may be important in explaining edge responses in butterflies (Siu *et al.* 2016). This could be important if traffic (ca. 270,000 vehicles per year between May and November, Großglockner Hochalpenstraßen AG pers. comm., 2013) were to be limited for nature management purposes.

Material and methods

Study area

This study was carried out in the Hohe Tauern National Park in Austria, in grassland habitats located at elevations of 1,850 to 2,400 m a.s.l. from 12.vii.2013 to 12.viii.2013. The Hohe Tauern National Park comprises many habitats important to Ringlet butterflies, such as different types of grassland and dwarf shrub heaths, and 21 *Erebia* species are known to occur within its boundaries (Huemer and Wieser 2008). We selected 8 study plots on grassland sites on the north facing side of the national park which is situated in the province of Salzburg (see Figure 1), coordinates of the sites in longitude/latitude were as follows: A = 47.1220°N/12.8240°E, B = 47.1213°N/12.8237°E, C = 47.1188°N/12.8269°E, D = 47.1202°N/12.8242°E, E = 47.1300°N/12.8065°E, F = 47.1284°N/12.8050°E, G = 47.1296°N/12.8060°E, H = 47.1258°N/12.8083°E. These plots were of similar physical structure and relatively homogeneous with respect to slope and nectar resources with only small parts of open soil and rocks interspersed but differed in the habitat boundaries to which they were adjacent. They ranged from 20 to 100 metres in length and 10 to 100 metres in width, depending on the local conditions. Each plot bordered one of the four boundary types on one side and grassland on the other side, so that each boundary type was replicated once. The four boundary types are: shrubs (=dwarf shrub heaths, mostly comprising species of *Rhododendron* L., *Vaccinium* L. and *Juniperus* L.), scree



Figure 1. Map of the study site with the locations where butterflies were observed.

(= barely vegetated stony areas), trees (= isolated stands in the generally low vegetated landscape, usually spruce *Picea abies* (L.) H. Karst. in the region), and the asphalt road (= a large road of an average width of 8 m) cutting across the national park. The road was built in 1935 and is intensively used by motorized traffic during the summer season. All plots were inhabited by *Erebia* adults (which we had verified by observations the previous year). These were observed across the whole of each respective plot.

Study system: *Erebia* butterflies

Ringlets are univoltine or semivoltine species with adults flying from May to September, depending on species and altitude. The larvae feed on grasses or sedges, and in many alpine species the development takes two years (Sonderegger 2005). Often several *Erebia* species occur sympatrically, which is why we chose them for this study. Possible differences in reaction to edge type are unlikely to result from phylogenetic origin, as the morphology and physiology of these butterflies are, apart from body size and minor differences in wing patterns, very much alike. This makes the genus an excellent system for studying edge permeability across multiple species in an alpine landscape.

Behavioural data

To analyse a butterfly's response to habitat edges, we used a variation of the point-release approach (e.g., Schultz et al. 2012; Kallioniemi et al. 2013). We checked plots across the whole width and length for butterflies engaging in flight towards a bordering structure. As soon as a butterfly moved towards

a bordering structure, we recorded its behaviour. If there were still butterflies on a site that did not engage in flight towards a boundary after that, we did not include these individuals and moved on to the next site. Only spontaneously flying individuals were chosen for observation. Butterflies that nectared at the time we discovered them were not included in the analysis, as the intake of nectar might have influenced their subsequent behaviour. Then we recorded if the butterfly crossed the border or not, assigning a score of 1 or 0, respectively. After observing the edge-mediated behaviour of a butterfly, it was caught with a hand-held net and species identity and sex were determined. Age was estimated by wing-wear on a rank scale (1 = fresh, 2 = wings slightly fringed, 3 = pieces of wing missing, 4 = highly damaged wings; this is a commonly used approach to estimate butterfly age, e.g. Walters *et al.* 2012). Butterflies were released immediately after handling at the point of capture, viz. on either side of the respective boundary. Thus, only an individual's complete crossing behaviour was assigned to a score of 1, and a score of 0 was assigned if it engaged in a u-turn and stayed on the site; an individual that entered the boundary but did not cross was also classified as 0. In this way, the butterfly's flight remained natural and un-manipulated during the behavioural decision. Dispersing butterflies coming from outside and leaving the respective site were not included in the analysis. For every butterfly, we noted date and time of capture. All observations were carried out by the same observer. Depending on the weather conditions and thus the butterflies' activity, each site was visited daily (in total between 4 and 12 visits per site) and the observation time per visit ranged from 30 minutes up to 1 hour per site. Observations were carried out between 9:00 and 17:00, according to the butterflies' activity. Observations only took place during fair weather conditions, i.e. during sunny to partly cloudy weather when butterflies were active. A few observations ($N < 5$) that occurred during periods of strong winds, which might have caused accidental dispersal of individuals, were not included in the analyses.

Statistical analyses

For statistical analyses, the incidences of the crossing (1) vs. the avoidance of boundaries (0) were used. Generalised linear mixed models (GLMM) with binomial error structure were implemented for analysing the likelihood of crossing between the different boundary types (modelled as fixed factors). Species affiliation was included as random factor to take into account the potential behavioural differences between the species involved. The analyses were performed in the R environment (R Core Team 2017) using the package lme4 (Bates *et al.* 2015). Explained variance through fixed effects, as well as fixed plus random effects, were expressed as marginal and conditional R^2 values. Further, generalised linear models (GLM), also with binomial error structure, were used to analyse possible differences between species. For *Erebia pandrose* (Borkhausen, 1788), for which we had substantially more observations than for all other species, the likelihood of crossing was further analysed with GLMs regarding the time of the day (categorical fixed factor with morning defined as the time between 9:00 and 11:00, midday between 11:00 to 15:00 and afternoon after 15:00) and the potential differences between the two un-vegetated border types, road and scree. Graphical representations of the results were obtained using the package ggplot2 (Wickham 2009).

Results

Edge permeability

We captured 373 individuals (136F, 237M) belonging to 11 *Erebia* species (see Table 1), among which the largest proportion of individuals (239) belonged to *E. pandrose*. The number of observed

Table 1. Individuals observed per *Erebia* species (f = female, m = male), only individuals with more than 10 observations were used for further analyses.

Species	f	m	Captures	Sex-ratio
<i>E. aethiops</i>	2	1	3	2
<i>E. epiphron</i>	5	25	30	0.2
<i>E. eriphyle</i>	7	7	14	1
<i>E. euryale</i>	6	21	27	0.3
<i>E. gorge</i>	3	6	9	0.5
<i>E. ligea</i>	2	3	5	0.7
<i>E. manto</i>	4	0	4	
<i>E. melampus</i>	1	4	5	0.3
<i>E. nivalis</i>	4	10	14	0.4
<i>E. pandrose</i>	98	141	239	0.7
<i>E. pharte</i>	4	19	23	0.2
Total	136	237	373	

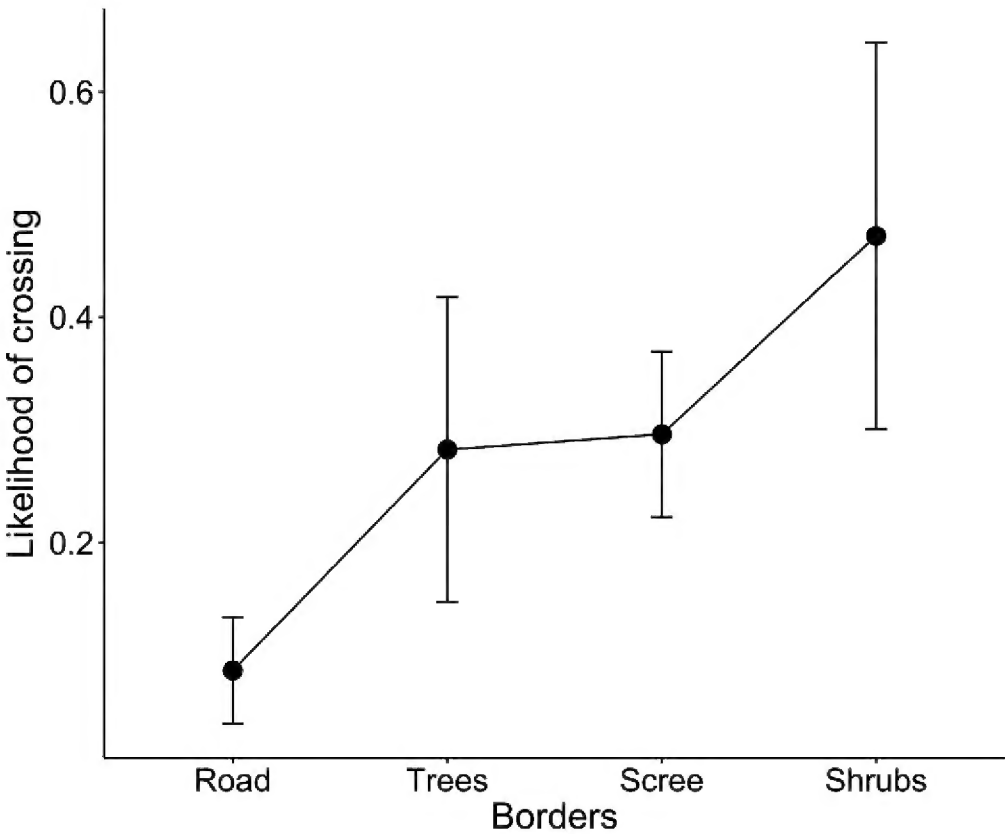


Figure 2. Permeability at four different edge types (road, scree trees, shrubs) for *Erebia* adults depicted as the proportion of individuals approaching an edge and crossing it, a likelihood of 0.1 means that 10% of individuals are likely to cross. Whiskers represent the confidence interval.

crossings was significantly different across edge types (Figure 2; Likelihood-ratio of fixed factor border-type: $\text{Chi}^2 = 9.569$; $p = 0.02$; $R^2_{\text{marginal}}/R^2_{\text{conditional}} = 0.08 / 0.50$). Permeability was lowest at the edge-type “road” for all species ($Z = -2.25$, $p = 0.02$), with a likelihood of crossing of less than 0.1, followed by “trees” and “scree” (< 0.4). “Shrubs” was most permeable for all studied species, but also here the likelihood of crossing scored below 0.5.

The total number of crossings differed significantly between species (Figure 3; $\text{Chi}^2 = 77.31$; $p < 0.001$; $R^2 = 0.19$). Among the species for which we had more than 10 observations, *E. euryale* (Esper, 1805) was most likely to cross a habitat edge (> 0.5), followed by *E. nivalis* Lorković & de

Lesse, 1954. *E. eriphyle* (Freyer 1836), *E. pandrose*, *E. pharte* (Hübner, 1803–1804) and *E. epiphron* (Knoch, 1783) were all similarly reluctant to cross an edge (< 0.25) (see Figure 3). Testing the permeability of “scree” versus “road” (both represent un-vegetated areas; $\text{Chi}^2 = 9.82$; $p = 0.002$; $R^2 = 0.05$) for *E. pandrose*, for which we had a sufficient number of observations to make a comparison, showed that the road was significantly less permeable (Figure 4; GLM: $Z = -6.98$; $p < 0.001$) than “scree” (GLM: $Z = 2.96$; $p = 0.003$). Gender and age did not noticeably affect crossing behaviour.

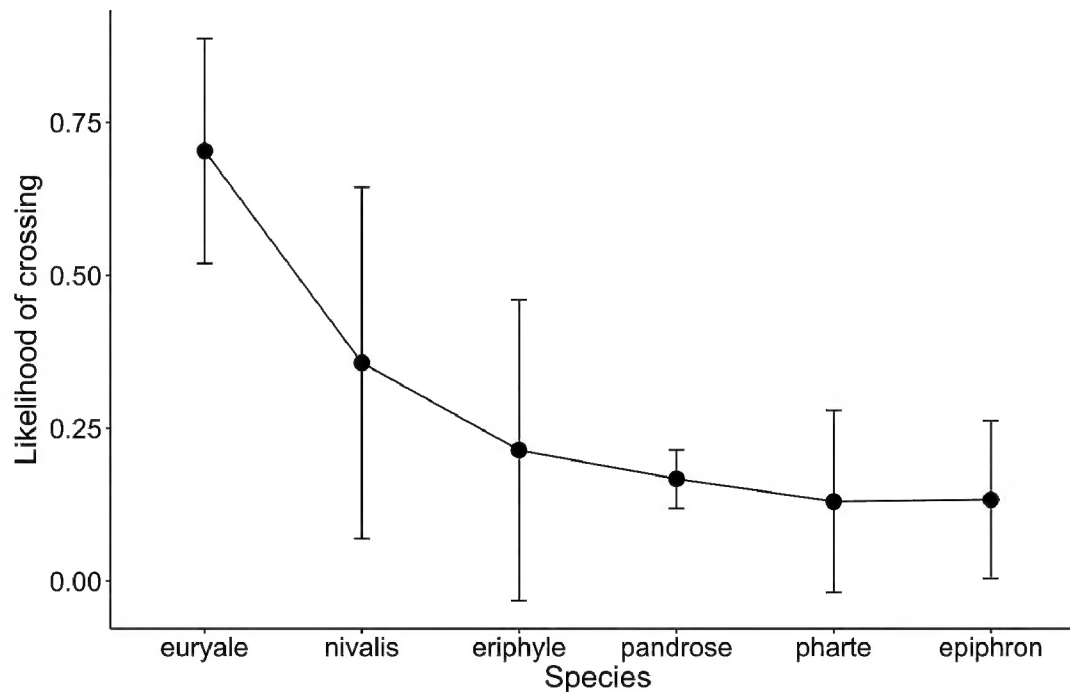


Figure 3. Likelihood of crossing any habitat edge when approaching it for six different *Erebia* species: *euryale*, *nivalis*, *eriphyle*, *pandrose*, *pharte*, *epiphron*, a likelihood of 0.1 means that 10% of individuals are likely to cross. Whiskers represent the confidence interval.

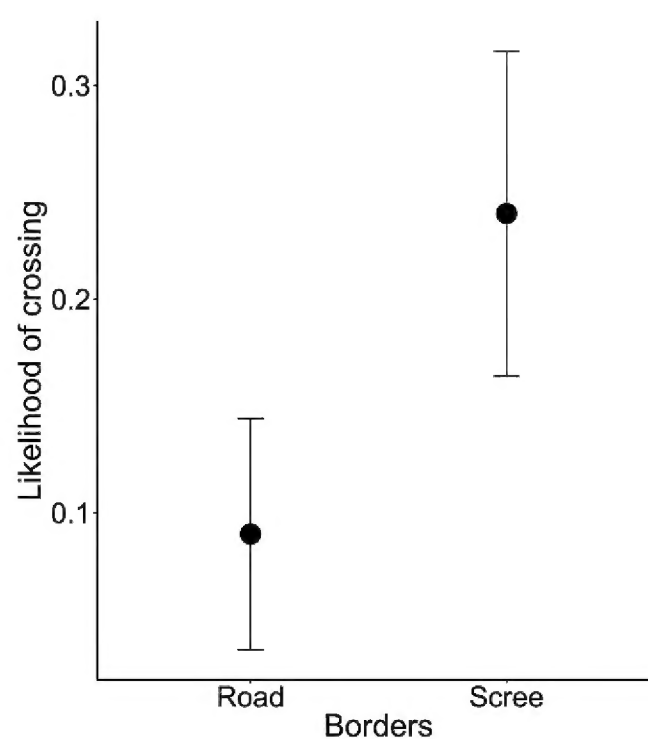


Figure 4. Permeability of an anthropogenic (road) versus a natural (scree) unvegetated habitat edge for *Erebia pandrose* adults, depicted as the proportion of individuals approaching and crossing it, a likelihood of 0.1 means that 10% of individuals are likely to cross. Whiskers represent the confidence interval.

Time-of-day effects

The time of day significantly affected the likelihood of crossing for *E. pandrose* individuals (GLM: $\text{Chi}^2 = 14.269$; $p < 0.001$; $R^2 = 0.07$). In the mornings (9:30–11:00; $Z = 0.65$; $p = 0.516$) and in the afternoon (after 15:00; $Z = -4.75$; $p < 0.001$) butterflies were more inclined to move across an edge than in the middle of the day (11:00–15:00; $Z = -2.84$; $p = 0.004$) (Figure 5). Using the whole data set (11 species) or only the smaller sized grassland species (*E. pharte*, *melampus* (Fuessly, 1775), *epiphron*, *manto* (Denis & Schiffermüller, 1775)), this pattern disappeared (Table 2). Generally, observations after 15:00 concerned mainly *E. pandrose*, the other Ringlet species had mostly already retreated to rest by that time.

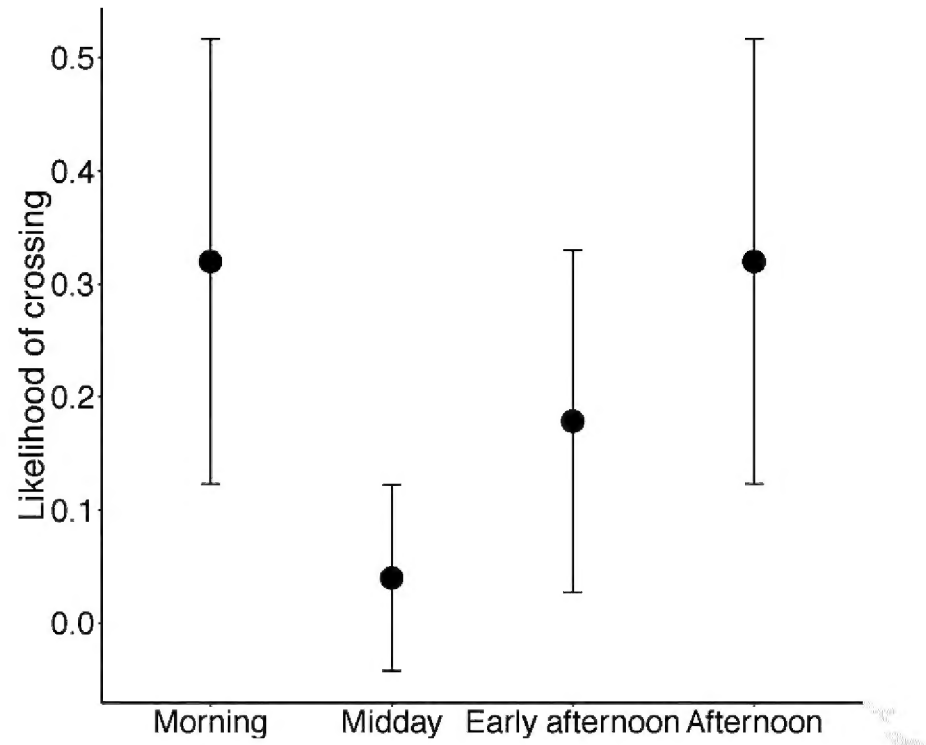


Figure 5. Likelihood of crossing a habitat edge when approaching it for the species *Erebia pandrose* in relation to the time of the day, a likelihood of 0.1 means that 10% of individuals are likely to cross. Whiskers represent the confidence interval.

Table 2. Edge permeability for *Erebia* butterflies as the proportion of individuals approaching an edge that cross in relation to time of day.

	Cross [1/0]	9:30–11:00 h	11:01–13:00 h	13:01–15:00 h	after 15:00 h	Sum
only <i>Erebia pandrose</i>	0	45	64	26	64	199
	1	16	1	5	18	40
	Sum	61	65	31	82	239
	Prob(cross)	0.26	0.02	0.16	0.22	0.17
smaller sized <i>Erebia</i> -species (<i>pharte</i> , <i>melampus</i> , <i>eriphyle</i> , <i>epiphron</i> , <i>manto</i>)	0	13	21	31		65
	1	3	5	3		11
	Sum	16	26	34		76
	Prob(cross)	0.19	0.19	0.09		0.14
All <i>Erebia</i> -species	0	63	93	66	64	286
	1	29	20	19	19	87
	Sum	92	113	85	83	373
	Prob(cross)	0.32	0.18	0.22	0.23	0.23

Discussion

Road and species effects

Our results support the hypothesis that the road has a far lower permeability for *Erebia* butterflies than naturally un-vegetated areas (scree, in our study); this effect was consistent across all studied Ringlet species and also consistent with our earlier findings (Polic *et al.* 2014). The road, however, was not a complete barrier since a few individuals of the species *E. pandrose* (10 individuals), *nivalis* (1) and *epiphron* (1) did cross (Table 3). Generally, all studied species avoided crossing habitat boundaries, natural and anthropogenic ones, similar to findings in other studies on the behaviour of butterflies at habitat edges (Polic *et al.* 2014; Mair *et al.* 2015).

Another key result from our study was that the likelihood of crossing habitat boundaries differed between species within the genus *Erebia*: *E. euryale* and *E. nivalis* were clearly more likely to leave a habitat patch than the other species. *Erebia nivalis* has been suggested to be a relatively good disperser in a mark-release-recapture study performed in the same year and in the same area as our study (Ehl *et al.* 2016), with a potential dispersal distance calculated to be up to five kilometres. Most individuals, however, are reported to be rather sedentary, similar to our findings. Those authors also reported that females of *E. nivalis* are less active fliers than males but are the ones more likely to undertake long-distance flights. In former mark-release-recapture work that compared the movement of six different *Erebia* species (*eriphyle*, *epiphron*, *pharte*, *gorge* (Hübner, 1803–1804), *pandrose*, *nivalis*) we found only *E. pharte* to be more likely to change between plots than the other Ringlet species (Polic *et al.* 2014). It is important to note that *Erebia* butterflies are generally rather sedentary, more than half of the individuals marked in this earlier experiment (Polic *et al.* 2014) did not move more than 25 metres between recapture events.

With regard to behavioural responses of other genera of butterflies at habitat boundaries, Mair *et al.* (2015) did not find differences between the likelihood of crossing for the three lycaenid species, *Polyommatus icarus* (Rottemburg, 1775), *Aricia agestis* (Denis & Schiffermüller, 1775) and *Plebejus argus* (Linnaeus, 1758). In their study, they observed behavioural responses that varied from ‘soft’ boundaries (= broadly similar vegetation structure) to ‘hard’ boundaries (= tall trees with few nectar sources). They found that activity levels within the habitat differed among the three species and concluded that the most active species in general are also the most likely to cross habitat boundaries. In our study, we cannot differentiate between activity and abundance, as we only observed the individuals that were actually moving and did not attempt to collect abundance measurements. Nevertheless, *E. pandrose* was obviously the most abundant species, but not the most likely to cross boundaries (see Figure 3).

In our data, edge type was decisive for the likelihood of crossing. When looking at the individual movements of *E. euryale* and *E. nivalis* (Table 3), we found that for the former species all movements across edges were directed towards trees or shrubs and for the latter species all crossing movements occurred towards scree or the road. This can be explained by the species’ ecology and habitat preferences: *E. euryale* is a montane species that lives in a variety of habitats. It inhabits open mountain forests from above 800 m up towards the tree-line, and is often associated with spruce forest clearings, but it can also occur in more exposed slopes and subalpine meadows. Therefore, trees or shrubs do not represent boundaries for *E. euryale*. The association with open woodland is most likely the reason for its readiness to cross the edge towards higher vegetation like trees and shrubs, an inclination that the other studied species entirely lacked. On the other hand, *Erebia nivalis*, a Ringlet species endemic to the eastern central Alps, is restricted to elevations above 1800 m, typically above the treeline, and

Table 3. Individual crossing behaviour per species (\uparrow = crossed; \cap = stayed on patch).

<i>E. pandrose</i>	\uparrow	\cap	total n(ind)	<i>E. epiphron</i>	\uparrow	\cap	total n(ind)	<i>E. euryale</i>	\uparrow	\cap	total n(ind)
scree	30	87		scree	2	6		scree	0	0	
road	10	109		road	1	20		road	0	0	
trees	0	2		trees	0	0		trees	12	7	
shrubs	0	1		shrubs	1	0		shrubs	7	1	
total (observations)	40	199	239		4	26	30		19	8	27
<i>E. pharte</i>	\uparrow	\cap		<i>E. eriphyle</i>	\uparrow	\cap		<i>E. nivalis</i>	\uparrow	\cap	
scree	0	0		scree	0	1		scree	4	5	
road	0	0		road	0	2		road	1	4	
trees	1	9		trees	0	6		trees	0	0	
shrubs	2	11		shrubs	3	2		shrubs	0	0	
total (observations)	3	20	23		3	11	14		5	9	14
<i>E. gorge</i>	\uparrow	\cap		<i>E. ligea</i>	\uparrow	\cap		<i>E. melampus</i>	\uparrow	\cap	
scree	9	0		scree	0	0		scree	0	0	
road	0	0		road	0	0		road	0	0	
trees	0	0		trees	0	5		trees	0	3	
shrubs	0	0		shrubs	0	0		shrubs	1	1	
total (observations)	9	0	9		0	5	5		1	4	5
<i>E. manto</i>	\uparrow	\cap		<i>E. aethiops</i>	\uparrow	\cap					
scree	0	0		scree	0	0					
road	0	0		road	0	0					
trees	0	1		trees	0	0					
shrubs	0	3		shrubs	3	0					
total (observations)	0	4	4		3	0	3				

occurs on barely vegetated sunny, rocky and often steep slopes with only patches of vegetation (Sonderegger 2005). It actively seeks barren areas for thermoregulation (R. Verovnik, pers. comm., 2019), and so scree and even the road constitute less of a barrier for this species than vegetated areas, like dwarf shrubs and trees. Thus, species that also live in the montane and subalpine zone, where forest is part of the natural habitat (*E. euryale*, *pharte*), are more inclined to fly across habitat borders comprising higher vegetation like trees or shrubs than species truly restricted to alpine areas (*E. nivalis*).

The fact that *E. pandrose* and *E. epiphron* were the most frequently sighted butterflies in our study is not too surprising *per se*. They are often reported to be the most abundant Ringlet species above the timberline (e.g., Cizek et al. 2003) and *E. epiphron* was also quite abundant in the previous year (Polic et al. 2014). It is surprising, however, that in the year before individuals of *E. pandrose* were among the least captured in the mark-release-recapture study (Polic et al. 2014) and only 34 individuals were marked during the entire season (between 7.vii. and 12.viii.). So it seems that 2013 was a particularly good year for *E. pandrose*.

The general avoidance of the asphalt road could be related to the lack of complex ground cover, which is perceived by the butterflies. Although we have no data on a butterfly’s view of anthropogenic infrastructural objects, we presuppose that large asphalted areas offer no place to hide, and are avoided by butterflies as crossing them would increase their predation risk. Besides, they are obviously also a resource free zone, i.e. a non-habitat. In the natural boundaries we studied there may be the occasional nectar source. As we know from earlier work (Polic et al. 2014) the presence of nectar sources affects movement behaviour of *Erebia* butterflies. We did not study the impact of traffic intensity on the permeability of the road, but following our field observations it seems likely that the sheer presence of asphalted ground hinders butterfly movement, and not the approaching vehicles.

Time effects

The likelihood of *E. pandrose* adults crossing a habitat edge peaked in the mornings and afternoons whereas it was much lower in the middle of the day. This behaviour probably reflects the daily activity patterns of the species. Other authors have also observed clear diurnal patterns in the behaviour of *Erebia* species (*E. epiphron* and *E. euryale*) in alpine grasslands in the Eastern Sudetes (Konvička *et al.* 2002) where they found that males were more active fliers than females and bask in the mornings, then patrol for mate-location as soon as it gets warmer with an activity peak just before noon and nectar in the afternoons, while mated females oviposit in the afternoons. This diurnal pattern seems to be characteristic for mountain *Erebia* adults (Konvička *et al.* 2002), as low temperatures seem to be the limiting factor for butterflies' activity in mountain and alpine habitats and the butterflies utilize each sunny moment for nectaring and mate location. For a lowland representative of the genus, like *E. aethiops* (Esper, 1777), however, high temperatures seemed to limit their flight activity (Slamova *et al.* 2010). This species was observed to spend the hottest part of the day in the shade, similar to our observations of *E. pandrose*.

Similar diurnal activity alterations were also observed for a number of other nymphalid butterflies (Grill 2003; Peixoto and Benson 2009), and are often related to an avoidance of stressful thermal conditions and to increase the chance to mate. In the case of two sympatric tropical satyrine butterflies (Peixoto and Benson 2009), one species showed a similar diurnal activity pattern to *E. pandrose*, with peaks in the morning and afternoon. In the other species, however, flight activity peaked at mid-day, probably due to their territorial behaviour. If territorial behaviour plays a role at all among the studied *Erebia* species, this was not evident in the field situation and could not be observed or quantified. Considering that *Erebia* species are generally cold-adapted (Slamova *et al.* 2010), and as solar radiation can be very strong on the slopes where our study was carried out, also the dark coloured *E. pandrose* may choose to rest during the hours of the day when the sun approaches its zenith in order to avoid overheating.

With the knowledge that crossing probability may change during the day, a time-frame (for example the morning hours) could be envisaged for limiting (or banning) traffic and providing temporal windows for butterflies to facilitate their crossing of the road during the hours when they are most active.

Conclusions

The most important finding of this study is that the road indeed represents the strongest barrier to the movement of *Erebia* butterflies among the studied habitat edges. Reluctance of *Erebia* butterflies to cross the road is probably related to the different texture of the road, not to the intensity of traffic (A. Grill, pers. observation). The road definitely reduces inter-patch exchange of *Erebia* butterflies in a large Austrian nature reserve.

Roads are thus not only affecting the home ranges of large animals, for which they are well known to alter landscape permeability (e.g., Wadey *et al.* 2018), but also for small flying insects, like butterflies, for which this may not be as obvious. Strategies to make roads more permeable have up to now mainly been implemented for vertebrates. Temporal closures, for example, have been shown to be beneficial for mammals in a Canadian national park (Whittington *et al.* 2019), and the installation of vegetated bridges has been highly beneficial for forest microbat communities in Australia (McGregor *et al.* 2017). In this case, the vegetated overpasses facilitate habitat continuity across a four-lane road separating two forest reserves near Brisbane for a wide range of species from small flying vertebrates to reptiles and amphibians. Similar structures would surely also enhance connectivity of habitats across asphalt roads for butterflies or other insects in the Hohe Tauern National Park.

Notably, our data suggest that for some Ringlet species the barrier effect of the road is more pronounced than for others. Species with high phenotypical similarity may behave quite distinctly when approaching habitat boundaries. Seeking a deeper understanding of the diversity of Ringlet butterflies along behavioural and ecological gradients seems therefore worthwhile, for example with regard to the fate of these emblematic alpine insects in response to ongoing climate and land-use change.

Acknowledgements

This work was supported by an Austrian Science Foundation (FWF) grant to Andrea Grill (V169-B17) and funds from the University of Vienna. Permits for handling *Erebia* butterflies were obtained from the regional government of Salzburg. We also thank five reviewers for their critical comments on the manuscript, which helped us to improve its clarity and style.

References

- Andersson P, Koffman A, Sjödin NE, Johansson V (2017) Roads may act as barriers to flying insects: species composition of bees and wasps differs on two sides of a large highway. *Nature Conservation* 18: 47–59. <https://doi.org/10.3897/natureconservation.18.12314>
- Ascensão F, Lucas PS, Costa A, Bager A (2017) The effect of roads on edge permeability and movement patterns for small mammals: a case study with Montane Akodont. *Landscape Ecology* 32: 781–790. <https://doi.org/10.1007/s10980-017-0485-z>
- Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecology* 22: 1117–1129. <https://doi.org/10.1007/s10980-007-9108-4>
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bergman P, Molau U, Holmgren B (1996) Micrometeorological impacts on insect activity and plant reproductive success in an Alpine environment. *Swedish Lapland. Arctic and Alpine Research* 28(2): 196–202. <https://doi.org/10.2307/1551760>
- Beyer HL, Gurarie E, Borger L, Panzacchi M, Basille I (2016) “You shall not pass!”: quantifying barrier permeability and proximity avoidance by animals. *Journal of Animal Ecology* 85: 43–53. <https://doi.org/10.1111/1365-2656.12275>
- Cizek O, Bakesová A, Kuras T, Beneš J, Konvička M (2003) Vacant niche in alpine habitat: the case of an introduced population of the butterfly *Erebia epiphron* in the Krkonoše Mountains. *Acta Oecologica* 24: 15–23. [https://doi.org/10.1016/S1146-609X\(02\)00004-8](https://doi.org/10.1016/S1146-609X(02)00004-8)
- Ehl S, Dalstein V, Tull F, Gros P, Schmitt T (2016) Specialized or opportunistic – how does the mountain endemic butterfly *Erebia nivalis* survive in its extreme habitats? *Insect Science* 25: 161–171. <https://doi.org/10.1111/1744-7917.12400>
- Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA, Swanson FJ, Turrentine T, Winter TC (2003) *Road ecology: science and solutions*. Island Press, Washington DC, 481 pp.
- Grill A (2003) *Endemism in Sardinia: evolution, ecology and conservation in the butterfly Maniola nurag*. PhD thesis, Netherlands, University of Amsterdam.
- Huemer P, Wieser C (2008) *Nationalpark Hohe Tauern – Schmetterlinge*. Tyrolia-Verlag, Innsbruck – Wien, 221 pp.
- Jacobson SL, Bliss-Ketchum LL, de Rivera, CE, Smith, WP (2016) A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere* 7 (4): e01345. <https://doi.org/10.1002/ecs2.1345>

- Kallioniemi E, Zannese A, Tinker JE, Franco AMA (2013) Inter- and intra-specific differences in butterfly behaviour at boundaries. *Insect Conservation and Diversity* 7(3): 232–240. <https://doi.org/10.1111/icad.12046>
- Konvička M, Beneš J, Kuras T (2002) Microdistribution and diurnal behaviour of two sympatric mountainous butterflies (*Erebia epiphron* and *E. euryale*): relations to vegetation and weather. *Biologia* 57: 223–235.
- Legagneux P, Ducatez S (2013) European birds adjust their flight initiation distance to road speed limits. *Biology Letters* 9(5): 20130417. <https://doi.org/10.1098/rsbl.2013.0417>
- Lima SL, Blackwell BF, DeVault TL, Fernández Juricic E (2015) Animal reactions to oncoming vehicles: a conceptual review. *Biological Reviews* 90(1): 60–76. <https://doi.org/10.1111/brv.12093>
- Magura T, Lövei GL, Tóthmérész B (2017) Edge responses are different in edges under natural versus anthropogenic influence: a meta-analysis using ground beetles. *Ecology and Evolution* 7: 1009–1017. <https://doi.org/10.1002/ece3.2722>
- Mair L, Thomas, CD, Franco AMA, Hill J (2015) Quantifying the activity levels and behavioural responses of butterfly species to habitat boundaries. *Ecological Entomology* 40: 823–828. <https://doi.org/10.1111/een.12248>
- Matos C, Petrovan S, Ward AI, Wheeler P (2017) Facilitating permeability of landscapes impacted by roads for protected amphibians: patterns of movement for the great crested newt. *PeerJ*. 2017(5): e2922. <https://doi.org/10.7717/peerj.2922>
- McGregor M, Matthews K, Jones D (2017) Vegetated fauna overpass disguises road presence and facilitates permeability for forest microbats in Brisbane, Australia. *Frontiers in Ecology and Evolution* 5: 153–162. <https://doi.org/10.3389/fevo.2017.00153>
- Muñoz PT, Torres, FP, Megías AG (2015) Effects of roads on insects: a review. *Biodiversity and Conservation* 24(3): 659–682. <https://doi.org/10.1007/s10531-014-0831-2>
- Ng CS, Des Brisay PG, Koper N (2019) Chestnut-collared longspurs reduce parental care in the presence of conventional oil and gas development and roads. *Animal Behaviour* 148: 71–80. <https://doi.org/10.1016/j.anbehav.2018.12.001>
- Peixoto PEC, Benson WW (2009) Daily activity patterns of two co-occurring tropical satyrine butterflies. *Journal of Insect Science* 9: 54. <https://doi.org/10.1673/031.009.5401>
- Polic D, Fiedler K, Nell C, Grill A (2014) Mobility of ringlet butterflies in high-elevation alpine grassland: effects of habitat barriers, resources and age. *Journal of Insect Conservation* 18: 1153–1161. <https://doi.org/10.1007/s10841-014-9726-5>
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Ries L, Debinski DM (2001) Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. *Journal of Animal Ecology* 70: 840–852. <https://doi.org/10.1046/j.0021-8790.2001.00546.x>
- Rytwinski T, Fahrig L (2015) The impacts of roads and traffic on terrestrial animal populations. *Handbook of road ecology*, In van der Ree R, Smith DJ, Grilo C (eds) Wiley Blackwell, Chichester, West Sussex, 237–246. <https://doi.org/10.1002/9781118568170.ch28>
- Schultz CB, Franco AMA, Crone EE (2012) Response of butterflies to structural and resource boundaries. *Journal of Animal Ecology* 81: 724–734. <https://doi.org/10.1111/j.1365-2656.2011.01947.x>
- Siu JC, Kosciński D, Keyghobadi N (2016) Swallowtail butterflies show positive edge responses predicted by resource use. *Landscape Ecology* 31: 2115–2131. <https://doi.org/10.1007/s10980-016-0385-7>
- Slamova I, Klecka J, Konvička M (2010) Diurnal behaviour and habitat preferences of *Erebia aethiops*, an aberrant lowland species of a mountain butterfly clade. *Journal of Insect Behavior* 24: 230–246. <https://doi.org/10.1007/s10905-010-9250-8>
- Sonderegger P (2005) Die Erebie der Schweiz (Lepidoptera: Satyrinae, genus *Erebia*). Eigenverlag Peter Sonderegger, Brugg, Switzerland, 712 pp. [73 pls]

- van der Ree R, Smith DJ, Grilo C (2015) Handbook of Road Ecology. Wiley Blackwell, Chichester, West Sussex, 522 pp. <https://doi.org/10.1002/9781118568170>
- Wadey J, Beyer HL, Saaban S, Othman N, Leimgruber P, Campos-Arceiz A (2018) Why did the elephant cross the road? The complex response of wild elephants to a major road in Peninsular Malaysia. *Biological Conservation* 218: 91–98. <https://doi.org/10.1016/j.biocon.2017.11.036>
- Walters JR, Stafford C, Hardcastle TJ, Jiggins CD (2012) Evaluating female remating rates in light of spermatophore degradation in *Heliconius* butterflies: pupal-mating monandry versus adult-mating polyandry. *Ecological Entomology* 37: 257–268. <https://doi.org/10.1111/j.1365-2311.2012.01360.x>
- Whittington J, Low P, Hunt B (2019) Temporal road closures improve habitat quality for wildlife. *Scientific reports* 9: 3772. <https://doi.org/10.1038/s41598-019-40581-y>
- Wickham H (2009) ggplot2: elegant graphics for data analysis. Springer, New York, 212 pp. <https://doi.org/10.1007/978-0-387-98141-3>